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Phylogenetically diverse grasslands are associated with pairwise interspecific processes that increase biomass

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Abstract. Biodiversity is an important determinant of primary productivity in experimental ecosystems. We combine two streams of research on understanding the effects of biodiversity on ecosystem function: quantifying phylogenetic diversity as a predictor of biodiversity effects in species-rich systems and the contribution of pairwise interspecific interactions to ecosystem function. We developed a statistical model that partitions the effect of biodiversity into effects due to community phylogenetic diversity and other community properties (e.g., average pairwise interaction, between- and within-functional-group effects, and so forth). The model provides phylogenetically based species-level explanations of differences in ecosystem response for communities with differing species composition. In two well-known grassland experiments, the model approach provides a parsimonious description of the effects of diversity as being due to the joint effect of the average pairwise statistical interaction and to community phylogenetic diversity. Effects associated with functional groupings of species in communities are largely explained by community phylogenetic diversity. The model approach quantifies a direct link between a measure of the evolutionary diversity of species and their interactive contribution to ecosystem function. It proves a useful tool in developing a mechanistic understanding of variation in ecosystem function.

Key words: biodiversity-ecosystem-function; community phylogenetic diversity; diversity–interaction model; ecosystem function; grassland ecosystem; phylogenetic distance; phylogenetic diversity; strength of interaction.

Introduction

Given their importance in the global economy, understanding how diverse biological communities contribute to ecosystem functioning is a central issue for ecological science. There is a developing realization that species interactions and niche differences affect ecosystem functioning and have strong roots in evolutionary history (Cavender-Bares et al. 2009). Quantifying the relationship between species interactions and their evolutionary divergence is one of the challenges facing ecology in developing a predictive science to manage the effects of change on communities. This is particularly pressing in the face of global change that is mediating major shifts in ecosystems and increasing threats to species.

Biodiversity can positively influence ecosystem functioning in experimental communities (Hooper et al. 2005, Balvanera et al. 2006) across producers, herbivores, detritivores, and predators, and in aquatic and terrestrial ecosystems (Cardinale et al. 2006). Ecosystem functioning can be affected by the identities of species in the community, interactions among them, and their traits and phylogeny (Naeem et al. 2009). Here we outline a modeling approach to quantify and compare several of these contributors to ecosystem function.

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Diversity–interaction models (Kirwan et al. 2007, 2009, Hector et al. 2009) characterize functional responses for a mixed-species community as due largely to an identity effect (an appropriate average of the monoculture performance of species) and a diversity effect that is the aggregate effect of interactions between species in the community. Models within this framework describe pattern in the pairwise interactions (e.g., due to functional grouping, species-specific interaction propensity, et cetera) in terms of a small number of coefficients (Kirwan et al. 2009). These models have been used in understanding the diversity effect in a number of plant and invertebrate assemblages (Sheehan et al. 2006, Kirwan et al. 2007, Frankow-Lindberg et al. 2009, Nyfeler et al. 2009, O'Hea et al. 2010).

Generally analyses have not distinguished between the effects of minor vs. major differences among communities in either species composition (i.e., the identity of species in the community) or species' relative abundances (Hector et al. 1999, Schmid et al. 2002). By contrast, diversity–interaction models provide a detailed quantitative analysis of differences in responses between communities with the same richness, but different species composition and different relative abundances (Fig. 1). At a given level of richness, communities containing mostly the same species (at the same relative abundance) would tend to have similar diversity effects since they contain largely the same pairwise species interactions, whereas communities with the same richness but quite different (distantly related) species might have quite dissimilar diversity effects, as they depend on different sets of pairwise interactions. Equally, the effects of major changes in relative abundance across communities with identical species are inadequately addressed when composition is treated as a categorical variable, i.e., each possible subset combination of species is treated as a level of the categorical variable (e.g., Hector et al. 1999). In the diversity–interaction model, communities with above-average productivity at a given level of richness contain, on average, species with stronger-than-average positive interactions (Kirwan et al. 2007).

Why do pairwise interactions differ for different species combinations and how do they combine to produce diversity effects? Many indices measure differences between pairs of species, including standardized single-trait measures and multi-trait multivariate measures (e.g., Villeger et al. 2008, Cadotte et al. 2009). The trait and functional differences among species are the product of their evolutionary histories. Measures of evolutionary divergence may represent the various structural, physiological, life history, and biochemical features of species that have been the focus of evolutionary selection pressures, and which presumably contribute to a species' current ability to interact with other species. A premise of recent work is that measures of phylogenetic distance can be related to differences in phenotypic and ecological characteristics among species (Maherali and Klironomos 2007, Cadotte et al. 2008, 2009, Cavender-Bares et al. 2009, but see Cahill et al. 2008). Thus, the greater the amount of time since two species shared a common ancestor, the more trait or niche differences will have accumulated. Cadotte et al. (2008) found across 29 multispecies plant experiments that a measure of phylogenetic distance between communities was a better predictor of aboveground community biomass than number of species or functional groups. We developed an index of community phylogenetic diversity that combines a continuous measure of phylogenetic distances among the component species of communities with their relative abundance in the community and incorporate this into diversity–interaction models to provide a parsimonious explanation of the diversity effect.

Some plant functional groups have a strong phylogenetic underpinning (Edwards et al. 2007), and thus community productivity differences associated with these groupings may potentially explain phylogenetic diversity relationships and vice versa (Maherali and Klironomos 2007, Cadotte et al. 2008). Where functional group effects provide a good description of the biodiversity–ecosystem–function relationship, can variation among the functional group coefficients in the model be partly or wholly explained in terms of community phylogenetic diversity? There may be room for additional explanations as functional groups have been shown to have limited power to account for variation in productivity (Wright et al. 2006).

Where the function examined is community aboveground biomass, we illustrate the capacity of the model approach to address hypotheses such as the following: (1) The contribution of all pairwise interactions between species in a community largely explains the diversity effect in the biodiversity–ecosystem–function relationship, (2) community phylogenetic diversity is a significant contributor to this explanation, and (3) effects of functional groups and community phylogenetic diversity on the diversity effect are associated. We investigated these hypotheses using data from a nine-species experiment in Jena, Germany (Roscher et al. 2004) and data on 10 species from the Irish site of the Biodepth experiment (Hector et al. 1999).

Materials and Methods

Model description

The diversity–interaction model (Kirwan et al. 2007, 2009) describes the relationship between the functional response for communities and the sown relative abundance of species in the community. Suppose that the species pool contains s species from which communities of various levels of richness may be constructed. P_i and P_j are the initial proportions of the ith and jth species in the community ($P = 0$ if the species is not in the community). The following model describes the functional response (y) in a community with t species, ($t \leq s$), selected from the pool of s species. Only t of the

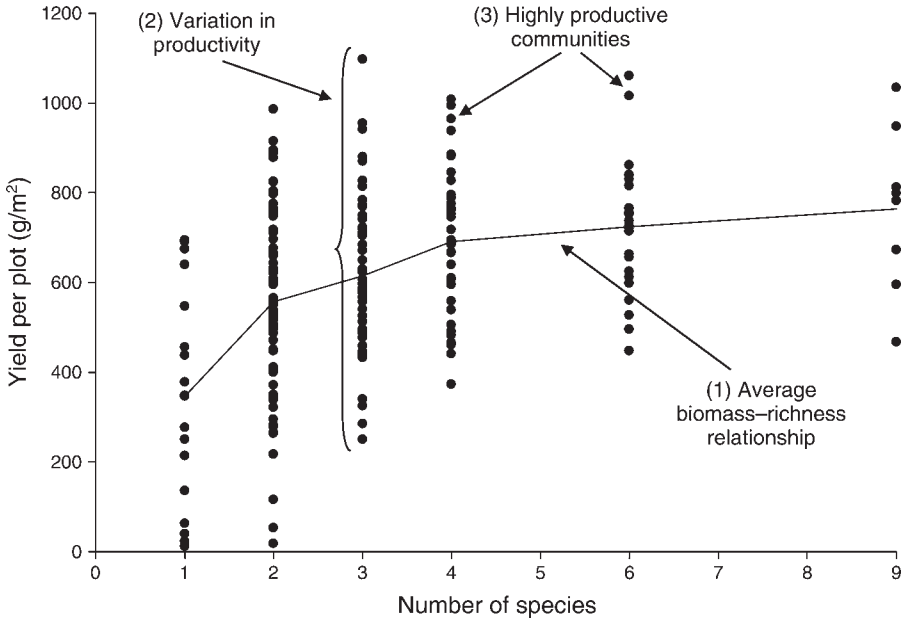

FIG. 1. Richness–productivity relationship for Jena, Germany, and the explanatory ability of the diversity–interaction model. (1) Typical analyses of biomass–richness relationships test for an average effect on productivity. (2) Such analyses offer little mechanistic explanation of the variation in productivity at each level of richness, which the diversity–interaction model does by modeling pairwise species interactions and identity effects. The variation between communities of equal richness arising from pairwise interactions is, in part, determined by evolutionary differences. Communities consisting mainly of similar or closely related species result in lower biomass production than combinations of more disparate or distantly related species. (3) With such a mechanistic underpinning, researchers could predict combinations that result in high productivity.

proportions P_i will be nonzero for this community:

$$y = \sum_{i=1}^{s} \beta_i P_i + \sum_{i<j}^{s} \delta_{ij}(P_i P_j) + \varepsilon. \quad (1)$$

Here β_i is the functional response of the ith species in monoculture ($P_i = 1$) and is called its identity effect, and δ_{ij} reflects the potential of species i and j to produce an interaction effect (Kirwan et al. 2007, 2009). The relative abundance of the two species, P_i and P_j, scale this potential to give the expected contribution of that interaction to the functional response as $\delta_{ij}P_iP_j$. The contribution to the functional response from all pairwise interactions of species in a mixture, $\sum_{i<j}^{s} \delta_{ij}(P_iP_j)$, in model 1 is called the "diversity effect." In the absence of any diversity effect, the component $\sum_{i=1}^{s} \beta_i P_i$ of model 1 is the functional response: as in neutral communities, i.e., the response in a mixture would be an average of the identity effects of the component species weighted by species proportions. There may be patterns among the δ_{ij} (Kirwan et al. 2007, 2009) related to various biologically motivated hypotheses that could lead to a more parsimonious description of the diversity effect.

If δ_{av} is the average of all pairwise coefficients δ_{ij}, model 1 can be rewritten as

$$y = \sum_{i=1}^{s} \beta_i P_i + \delta_{av} \sum_{i<j}^{s} (P_iP_j) + \sum_{i<j}^{s} (\delta_{ij} - \delta_{av})(P_iP_j) + \varepsilon. \quad (2)$$

This partitions the diversity effect for the community into (1) an average effect $\delta_{av} \sum_{i<j}^{s}(P_iP_j)$, the average of all possible t species communities with the specified relative abundances of species, and (2) variation around this average at the particular level of richness of the community, $\sum_{i<j}^{s}(\delta_{ij} - \delta_{av})(P_iP_j)$. The sizes of these variations, for communities at a given level of richness, relate to differing compositions (and hence different pairwise species interactions) and to the relative abundances of species in the communities. The variations may also be related to trait based or phylogenetic measures of distances between species in the communities.

We explored whether phylogenetic distances between species in a community (D_{ij} for species i and j) can be used to explain differences between communities of differing species composition. We introduced a measure of community phylogenetic diversity (C_D) that incorporates these distances and species relative abundances for all the species in a community:

$$C_D = \sum_{i<j}^{s} (D_{ij} - \bar{D})(P_iP_j) \quad (3)$$

where $\bar{D}$ is the average of D_{ij} over all species in the species pool.

Including just the two terms, average species interaction and community phylogenetic diversity in the diversity effect gives the following model:

$$y = \sum_{i=1}^{s} \beta_i P_i + \delta_{av} \sum_{i<j}^{s} (P_i P_j) + \kappa C_D + \varepsilon. \quad (4)$$

The effect of variation in community phylogenetic diversity across communities at a particular level of richness is captured in the coefficient κ. When the community is dominated by species whose interspecific distances (D_{ij}) exceed their average ($\bar{D}$) (the community is dominated by more distantly related species from the overall pool of potential species), community phylogenetic diversity (C_D) will be positive. In this case, positive κ predicts a greater than average diversity effect, while communities dominated by closely related species will have negative community phylogenetic diversity, and will give a lower than average diversity effect.

More subtle models based on other partitions of the pairwise interaction coefficients δ_{ij} (Kirwan et al. 2009) may also be extended to include the effect of phylogenetic diversity. For example, the diversity effect among communities at a given level of richness can be modeled in terms of functional group coefficients (Kirwan et al. 2009). Assuming two functional groups gives the following model:

$$y = \sum_{i=1}^{s} \beta_i P_i + \delta_{bfg} \sum_{bfg} P_i P_j + \delta_{wfg_1} \sum_{wfg_1} P_i P_j + \delta_{wfg_2} \sum_{wfg_2} P_i P_j + \varepsilon. \quad (5)$$

All interaction coefficients between pairs of species with one from each of the two functional groups are assumed equal to δ_{bfg} (between functional group), and all interaction coefficients for pairs of species from within the first and second functional group are assumed equal to δ_{wfg1} (within functional group 1) and δ_{wfg2} (within functional group 2), respectively. Here, the summation $\sum_{bfg} P_i P_j$ is over all pairs of species with one from each of the two functional groups, and the within-functional-group terms are similarly defined. Where there are more than two functional groups, model 5 can be expanded to include separate coefficients for comparisons among the various functional groups and for a separate coefficient within each functional group. Adding a term κC_D extends this model to also include the effect of phylogenetic diversity. The statistical interaction coefficients and patterns among them provide parsimonious summaries of the ecosystem response data. Where there is a strong diversity effect the size and signs of these coefficients can help to suggest where mechanistic explanations (complementarity, facilitation, selection) should be sought.

Data

We tested these models using two data sets, from a biodiversity experiment at Jena, Germany (Roscher et al. 2004; see Plate 1), and from the Irish site in the Biodepth experiment (Hector et al. 1999).

Jena

Details are provided in Roscher et al. (2004). One hundred communities with one of six levels of species richness (1, 2, 3, 4, 6, and 9) were established in 206 plots laid out in four blocks. The species pool for the Jena experiment data set consisted of nine species from three functional groups: five grasses (*Dactylis glomerata*, *Phleum pratense*, *Alopecurus pratensis*, *Poa trivialis*, *Arrhenatherum elatius*), two nonlegume herbs (*Geranium pratense* and *Anthriscus sylvestris*), and two legumes (*Trifolium repens* and *Trifolium pratense*). Each community was replicated twice. The experimental area was partitioned into four blocks, following a gradient of soil characteristics. Total seedling densities of 1000 viable seeds/m^2 were used. In all communities, species present were equally represented at sowing. All plots were weeded regularly. The functional response was yield (total aboveground biomass [g/m^2]) in the year following establishment (Fig. 1).

Biodepth Ireland

Details are provided in Hector et al. (1999). At the Irish site, 31 communities with one of five levels of species richness (1, 2, 3, 4, and 8 species) were established in 66 plots laid out in two blocks. The species pool for the current data from the Irish site contained 10 species (omitting communities with either *Cerastium fontanum* and *Taraxacum officinale*, since they appeared in a total of only four plots). Species were from three functional groups: four grasses (*Agrostis capillaries* (L), *Alopecurus pratensis*, *Anthoxanthum odoratum*, and *Holcus lanatus*), four nonlegume herbs (*Centaurea nigra*, *Plantago lanceolata*, *Ranunculus repens*, and *Rumex acetosa*), and two legumes (*Lotus pedunculatus* and *Trifolium repens*). Communities contained one, two, or three of these groups. Each level of species richness and functional group richness was represented by several different plant communities. In each community all species present were equally represented at sowing. The functional response was yield (aboveground biomass [g/m^2]) from the third year (Appendix A: Fig. A1).

We constructed a separate phylogeny for the species used in these two experiments (see Appendix B for full information on methods of phylogeny construction and a table of resulting phylogenetic distances between species for each experiment).

Statistical analysis

Models 2, 4, and 5 were fitted to the two data sets using multiple regression. Variants of models 2 and 5 that omit or add some terms were also fitted and are denoted 2, 2a, et cetera, in Table 1. A reference model (model 6) was fitted that includes a degree of freedom for each different community composition and also includes block effects. Model 6 includes all possible diversity or block effects, and so the residual mean square should contain no structure and be a true

TABLE 1. Results for a range of models fitted to the Jena, Germany, and Biodepth Ireland data.

Model number and description	Jena		Biodepth Ireland	
	Model df	RMS	Model df	RMS
2) All pairwise interactions	48	15 241	32	21 904
2a) Average interaction only (δ_{av})	13	19 204	13	30 824
2b) No interaction	12	30 341	12	61 874
4) Average interaction only + C_D	14	18 157	14	26 984
5) Functional groups	18	17 437	18	26 017
5a) δ_{av} + within functional groups			16	25 803
5b) δ_{av} + within functional groups + C_D			17	26 195
5c) Functional groups + C_D	19	17 524	19	26 091
6) Reference model	103	15 710	32	21 904

Notes: In the model descriptions, δ_{av} represents the inclusion of the average pairwise interaction effect, C_D represents the linear effect of community phylogenetic diversity, "functional groups" represent pairwise interactions between and within the three functional groups (grasses, nonlegume herbs, and legumes) and "within functional groups" represents pairwise interactions within each functional group. RMS is residual mean square. Models with numbers 2, 4, and 5 included are based on the equations for models 2, 4, and 5, respectively, and include block and identity effects. Model 6 is a reference model explained in the section *Data: Statistical analysis*. Tests between models are shown in Table 2.

measure of error. This residual mean square is a target for the various diversity models to achieve; if the residual mean square for a diversity model is as low as that from model 6 it provides evidence that the diversity model explains virtually all of the structure in the data. The residual mean square from model 6 was used as the denominator in tests to compare models (Table 2). All models fitted included block effects in addition to terms specified in the model description section of Table 1. Hypothesis testing was through F tests among hierarchical models. Further details on models and a worked example for the Jena data set are in a supplement, which also contains code using the statistical software SAS and R and data for implementing the worked example.

Community phylogenetic diversity is aliased with the interaction terms in model 2 (all pairwise interactions) and so cannot be added to that model. Not all pairwise interactions could be estimated for the Biodepth Ireland data; there are potentially 45 pairwise interactions among 10 species, but only 20 of these were estimable due to design restrictions.

RESULTS

Results were very similar for both sites (P values in what follows are for Jena and Biodepth Ireland, respectively, and details of calculation are in Table 2). Model 2 (all pairwise interactions) fitted as well as the reference model at both sites (smaller or equal residual mean square, model 2 vs. 6; Table 2), confirming Hypothesis 1. This implies that pairwise interaction effects among species (model 2 vs. 2b, $P < 0.001$ and $P < 0.001$; Table 2) explained virtually all of the diversity effect in ecosystem function, but with large numbers of degrees of freedom (36 and 20 for Jena and Biodepth Ireland, respectively). Fitting model 2a (an average pairwise interaction effect) greatly improved the model fit relative to model 2b (no interactions) (model 2a vs. 2b, $P < 0.001$ and $P < 0.001$; Table 2). There was an additional strong positive linear effect of community phylogenetic diversity (model 4 vs. 2a, $P < 0.001$ and $P = 0.003$; Table 2). Jointly, these two degrees of freedom explained much of the diversity effect, especially in Biodepth Ireland (model 2 vs. 4, $P = 0.004$ and $P = 0.097$; Table 2). Both these tests confirm the importance

TABLE 2. Details of tests among models in Table 1.

Term tested	Models compared	Jena			Biodepth Ireland		
		F	df numerator	P	F	df numerator	P
All pairwise vs. reference	2 vs. 6	0.91	55	0.638			
All pairwise interactions	2 vs. 2b	6.15	36	<0.001	5.93	20	<0.001
δ_{av}	2a vs. 2b	138.75	1	<0.001	77.95	1	<0.001
C_D	4 vs. 2a	14.02	1	<0.001	10.52	1	0.003
Remainder of pairwise interactions	2 vs. 4	2.02	34	0.004	1.67	18	0.097
Functional groups	5 vs. 2a	5.45	5	<0.001	3.51	5	0.011
Remainder of pairwise interactions	2 vs. 5	1.85	30	0.012	1.64	14	0.117
Functional groups	5c vs. 4	2.66	5	0.026	1.62	5	0.183
C_D	5c vs. 5	0.07	1	0.786	1.03	1	0.318
C_D	5b vs. 5a				0.3	1	0.586
Within functional groups	5a vs. 2a				5.23	3	0.004
Within functional groups	5b vs. 4				1.82	3	0.162

Note: The denominator in the F test is the residual mean square for the reference model, and denominator degrees of freedom for the tests are 103 and 34 for Jena and Biodepth Ireland, respectively.

PLATE 1. Some dominance plots of the biodiversity experiment in Jena, Germany, in 2007. Here, nine dominant grassland species were established on 206 plots with a diversity gradient from 1 to 9 species. Photo credit: A. Weigelt.

of phylogenetic diversity in explaining the diversity effect (Hypothesis 2). Including terms for interactions between each pair of functional groups and for within each of the three functional groups (Kirwan et al. 2009) added to the explanatory power of the average interaction effect (model 5 vs. 2a, $P < 0.001$ and $P = 0.011$; Table 2). Jointly, average pairwise interaction and functional group effects explained most of the diversity effect, especially in Biodepth Ireland (model 2 vs. 5, $P = 0.012$ and $P = 0.117$; Table 2). Functional group effects were largely captured by community phylogenetic diversity in a single degree of freedom; including functional groups in addition to community phylogenetic diversity somewhat improved the fit only in Jena (model 5c vs. 4, $P = 0.026$ and $P = 0.183$; Table 2). The linear effect of community phylogenetic diversity did not add to the functional groups effect (model 5c vs. 5, $P = 0.786$ and $P = 0.318$; Table 2). These tests confirm the strong relationship between functional groups and community phylogenetic diversity (Hypothesis 3), with the latter capturing most of the functional group effect in a single degree of freedom. Results from the Jena data are explained and presented in further detail in the Supplement.

In the Biodepth Ireland data, the relationship between community phylogenetic diversity and functional groups was complex. Within-functional-group effects were significant when added to the average pairwise interaction (model 5a vs. 2a, $P = 0.004$), and community phylogenetic diversity did not add significantly to within-functional-group effects (model 5a vs. 5b, $P = 0.586$; Table 2), whereas it was significant when added to the model including just between-functional-group effects and the average pairwise interaction effect ($P = 0.010$, analysis not shown). Nor were within-functional-group effects significant when added to the model with community phylogenetic diversity (model 5b vs. 4, $P = 0.162$; Table 2). These results suggest that the linear effect of community phylogenetic diversity was associated with within-functional-group effects. These patterns were not observed in the Jena data.

For Jena, although the all pairwise interactions model fitted as well as the reference model, there was evidence of quadratic effects of community phylogenetic diversity ($P = 0.001$) and a quadratic average interaction ($P = 0.005$) when these terms were jointly added to model 2 (results not shown).

The effect of differences in phylogenetic diversity between communities of the same richness can be estimated. For model 4, the predicted average diversity effect at sown richness 4 (as an example) was 347 and 392 g/m^2 for Jena and Biodepth Ireland, respectively. The estimates of κ, the coefficient of community phylogenetic diversity, were 1235 and 1984 g/m^2 per unit of C_D, respectively. Since the estimate of κ was positive for both data sets, the predicted diversity effects from model 4 will fall above (below) the average diversity line when community phylogenetic diversity is positive (negative). A 3× standard deviation difference in community phylogenetic diversity between four-species communities corresponds to a change in

predicted diversity effect of size 78 and 95 g/m^2, respectively (Appendix C).

Discussion

The extent to which measures of evolutionary diversity (measured by phylogenetic distances) can predict patterns in ecosystem responses is a question of considerable current interest (Cadotte et al. 2008, Cavender-Bares et al. 2009). In a recent comprehensive review, Cavender-Bares et al. (2009) emphasized the importance of model-based approaches to determining the role of phylogenetic distance in community assembly, structure, and ecosystem response. Here we show how the diversity interaction method can be extended to jointly attribute effects of diversity to several sources using standard regression tools. In two landmark data sets, most of the effects of diversity were associated with community phylogenetic diversity, average pairwise interaction among species, and functional group diversity.

In both experiments, pairwise interaction effects among species explained virtually all of the effects of biodiversity on ecosystem function, but with large numbers of degrees of freedom (36 and 20 for Jena and Biodepth Ireland, respectively; Hypothesis 1). Just two degrees of freedom, one each for an average interaction effect and community phylogenetic diversity, accounted for most of this variation. At the same level of richness and relative abundance, more phylogenetically diverse communities were associated with processes that capture greater resources (Hypothesis 2). In both experiments there was considerable explanatory power associated with functional groups in addition to an average interaction effect. However, explanations provided by functional grouping and community phylogenetic diversity largely overlapped. Functional grouping explained marginally greater variation than community phylogenetic diversity in Jena but not in Biodepth Ireland, and community phylogenetic diversity did not add to the explanation provided by functional grouping in either data set (Hypothesis 3). Differences in the phylogenetic distance measure (C_D) for two communities at the same richness level can lead to appreciable differences in the diversity effect.

Community phylogenetic diversity perhaps provided a more refined explanation than functional group effects. The diversity effect was primarily associated with within-functional-group effects in Biodepth Ireland, but not for Jena. The species pool at the Irish Biodepth site included a *Ranunculus* species that was most distantly related to all other species (Appendix A: Fig. A2.1), and yet was included in the forb functional group, perhaps explaining the association of the community phylogenetic diversity effect with the within-functional-group component.

While our results here show that community phylogenetic diversity and functional groups convey overlapping information, it cannot be assumed that other phylogenetic topologies will also be synonymous (Cadotte et al. 2008). Our current data sets generally contain representatives from the major temperate herbaceous functional groups, but only limited variation within groupings, and very few congenerics, for example. Multiple data sets, with differing phylogenetic topologies and functional groupings, will help to distinguish whether the effect of community phylogenetic diversity is driven by associations of distances with functional grouping or if community phylogenetic diversity also encapsulates additional functional or niche differences.

The proposed methods were illustrated using data from well-structured experiments. Though desirable to improve efficiency of coefficient estimation, neither the inclusion of monocultures, nor a balanced design structure (in terms of richness and composition) are absolute requirements. The methods can be applied to data from natural systems, but they would require a reasonably wide range of communities to provide a solid base for model estimation.

We have shown that models based on community phylogenetic diversity and average pairwise interactions have high predictive ability. This is despite the underlying mechanisms of resource acquisition, functional traits, or the characteristics of their evolutionary history being unknown. Although our models are primarily descriptive, they are based on underlying biologically motivated factors and patterns of interspecific interaction. Our approach can be used to generate testable hypotheses. For example, to investigate resistance to invasion by a new species, community phylogenetic diversity could be systematically manipulated as an experimental variable, across a range of native and nonnative species.

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APPENDIX A

Yield per plot vs. number of species for the Biodepth Ireland experiment (*Ecological Archives* E092-116-A1).

APPENDIX B

Detail of the construction of the matrices of phylogenetic distances used for the species in the two experiments (*Ecological Archives* E092-116-A2).

APPENDIX C

Calculation of the standard deviation of the variable C_D across all communities at a given level of richness (*Ecological Archives* E092-116-A3).

SUPPLEMENT

Detailed description of how the methods are applied to data, including SAS and R code and data from two experiments (*Ecological Archives* E092-116-S1).